

Mitogenomes of the two historical species *Seira ferrarii* Parona, 1888 and *Seira pallidipes* Reuter, 1895 (Collembola, Entomobryidae, Seirinae) with their phylogenetic placement within Seirinae

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Abstract

The present paper reports the first occurrence of *Seira ferrarii* Parona, 1888 from Hungary. On this occasion, molecular analyses were performed on both *S. ferrarii* and another historical species of the genus, *S. pallidipes* Reuter, 1895, originally described from Hungary. Using low-coverage whole-genome sequencing, the complete mitogenomes were assembled and annotated using MitoZ. To test the phylogenetic placement of both species, we performed maximum likelihood and Bayesian analyses using a matrix containing 14 Seirinae species and two outgroups. Both resultant trees showed that the European populations of the sampled *Seira* spp. likely derive from ancestral branches of Seirinae, compared to the Asian and American populations. Our results put in question the monophyly of the genus *Seira*, as already observed in previous studies.

Key words: Entomobryoidea, Europe, gene order, Hungary, mitochondrial genomes, phylogeny, springtails



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Introduction

Although *Seira* Lubbock, 1870 is one of the most widespread genera of Entomobryidae worldwide, its high species richness is mainly found in the tropics (e.g., Mari Mutt 1986; Cipola et al. 2014, 2018b; Godeiro and Bellini 2014), with relatively few representatives occurring in Europe, most of which found in Mediterranean countries, under subtropical climates (e.g., Gama 1964; Tosi and Parisi 1990; Cipola et al. 2018a).

Seira ferrarii Parona, 1888 was originally described from Italy (Genova), and later also recorded in the Spanish mainland (Yosii 1959), Bulgaria, French mainland, Greek mainland, Malta, Republic of Moldova, Spain, Portugal, Romania, various islands (Canary Is., Corsica, Dodecanese Is., Sicily) (Bedos 2023), North Africa (Jacquemart and Jacques 1980; Barra 2004), and Israel (Gruia et al. 2000). From the capital of Hungary, Loksa and Loksa (1994) reported the presence of a “particular” *Seira* sp. juv., which however remained undetermined. On revisiting the sampling site, we managed to collect several specimens of this

abovementioned *Seira* sp., which were identified as *S. ferrarii*, and thus represent the first occurrence of the species in Hungary.

Seira pallidipes Reuter, 1895, on the other hand, was originally described from Hungary, and was recently redescribed and synonymized with *S. pillichii* Stach, 1929 by Winkler and Dányi (2017). Outside Hungary, the species occurs only in Austria and Serbia (Bedos 2023).

Seira dollfusi Carl, 1899 is a widely distributed species in Europe (Bedos 2023). However, as its true identity is unclear (the species has not yet been redescribed in detail based on type material or specimens collected at the type locality), we refer to specimens collected in Hungary for our study as *S. cf. dollfusi*.

The main goal of our study was to investigate for the first time the phylogenetic position of three European species of Seirinae. Previous studies focused on the Neotropical region (Godeiro et al. 2020) and the most embracing was recently published, containing species from the Neotropics and Asia (Godeiro et al. 2023). The internal organization of the subfamily is uncertain, and extensive taxon sampling is currently underway to propose a global phylogenetic study with dispersion routes and possible new genera.

Materials and methods

Specimens of *S. ferrarii* were collected in a xerophilous dolomite-steppe meadow association, Tétényi Plateau, Budapest, Hungary (47°25'6"N, 18°56'58"E, 195 m a.s.l.) on 7.X.2022 (leg. D. Winkler & M. Korda), while specimens of *S. pallidipes* were collected in a secondary hay meadow, Sopron, Hungary (47°45'31"N, 16°36'58"E, 169 m a.s.l.) on 4.VI.2022 (leg. D. Winkler). *Seira cf. dollfusi* was sampled on a calcareous open rocky grassland, Zuppa-tető, Szárliget, Hungary (47°30'10"N, 18°30'52.41"E, 359 m) on 6.IX.2022 (leg. D. Winkler).

On each occasion, an entomological aspirator was used for collection. Specimens were stored in absolute ethanol until further analysis. A Zeiss Stemi 508 stereomicroscope was used to sort the material. Habitus of the two studied species was photographed with a Canon EOS 7D digital camera attached to the stereomicroscope using a C-mount adapter.

Specimens for morphological identification were cleared using Nesbitt's fluid and then mounted on permanent slides in Hoyer's medium, following the protocol described by Jordana et al. (1997). The slides were examined under a Leica DM2500 LED microscope with conventional bright light and phase contrast.

Part of the material preserved in absolute ethanol was sent to Shanghai Yaoen Biotechnology Co., Ltd, China, where all laboratory experiments, including DNA extraction, amplification, and library construction were made according to the procedures suggested by the kits manufacturers. For DNA extraction, the TIANamp MicroDNA extraction kit (Tiangen Co., Ltd, China) was used. Libraries were constructed using KAPA Hyper Prep Kit (Roche, Basel, Switzerland). Approximately 10 Gbp of paired-end reads from each species were sequenced by an Illumina NovaSeq 6000 platform. This amount of data was enough to have a good coverage to assemble complete mitogenomes.

Mitogenomes were assembled, annotated, and visualized using MitoZ v.2.4-alpha (Meng et al. 2019). A manual check was necessary to confirm the start and end points of protein-coding genes (PCGs). Mitochondrial genome sequences with annotations and raw sequence data were submitted to the NCBI nucleotides

and SRA databases (<https://www.ncbi.nlm.nih.gov/>), with project number PRJ-NA971781. To complete our phylogenetic dataset, protein-coding genes (PCG's) of another 11 species of Seirinae and two Lepidocyrtinae (outgroups) were downloaded from NCBI (Table 1). The partial mitogenome of *S. cf. dollfusi* (9298 bp), also sequenced and assembled during the present study, was included in the phylogenetic analyses to test its closer relationship with *S. pallidipes*. The sequence is publicly available at: <https://doi.org/10.6084/m9.figshare.23654097>.

Previously to the alignment, nucleotide sequences of the 13 PCGs of the 16 species that comprise our phylogenetic dataset were translated into amino acids using TransDecoder v.5.5.0 (<https://github.com/TransDecoder/TransDecoder>). Previous phylogenetic studies of Collembola showed that due to the high heterogeneity of mitochondrial sequences, matrices created using amino acids produce better results than using nucleotides (Bellini et al. 2023; Godeiro et al. 2021). Also, according to a recent analysis, site-wise heterogeneity is typically a more significant source of bias in phylogenomic inference than protein-wise heterotachy (Wang et al. 2019; Yu et al. 2022). Independent files containing the PCGs were aligned by MAGUS (Smirnov and Warnow 2021) employing MAFFT (Kato et al. 2019). An automated alignment trimming was performed by BMGE v.1.12 (Criscuolo and Gribaldo 2010). PhyKIT v.1.9.0 (Steenwyk et al. 2021) concatenated the alignments and generated the partition scheme. The final matrix had 3104 amino acid sites and 13 loci.

To test the phylogenetic placement of the European species of *Seira*, we performed two phylogenetic inferences. IQ-Tree v.2.0.7 (Minh et al. 2020) was used to make the maximum likelihood (ML) analyses with 1000 ultrafast bootstrap replicates (Hoang et al. 2018) and SH-aLRT support (Guindon et al. 2010). The best model for each partition was suggested by ModelFinder (Kalyaanamoorthy

Table 1. Taxonomical information of the species used in the phylogenetic analyses. The newly assembled mitogenomes are represented in bold. *Mitogenome partially recovered. NA: not applicable.

	Species	Subfamily	Country	GenBank number
1	<i>Lepidocyrtus fimetarius</i> Gisin, 1964	Lepidocyrtinae	China	NC_047189.1
2	<i>Lepidocyrtus sotoi</i> Bellini & Godeiro, 2015	Lepidocyrtinae	Brazil	MT928545.1
3	<i>Lepidocyrtinus dapeste</i> Santos & Bellini, 2018	Seirinae	Brazil	MF716609.1
4	<i>Lepidocyrtinus harena</i> (Godeiro & Bellini, 2014)	Seirinae	Brazil	MF716617.1
5	<i>Seira atrolutea</i> (Arlé, 1939)	Seirinae	Brazil	MF716602.1
6	<i>Seira boneti</i> (Denis, 1948)	Seirinae	China	OP181099.1
7	<i>Seira brasiliiana</i> (Arlé, 1939)	Seirinae	Brazil	MF716619.1
8	<i>Seira dowlingi</i> (Wray, 1953)	Seirinae	Brazil	MF716615.1
9	<i>Seira cf. dollfusi</i>*	Seirinae	Hungary	NA
10	<i>Seira ferrarii</i>	Seirinae	Hungary	OR206048.1
11	<i>Seira pallidipes</i>	Seirinae	Hungary	OR115504.1
12	<i>Seira ritae</i> Bellini & Zeppelini, 2011	Seirinae	Brazil	MF716616.1
13	<i>Seira sanloemensis</i> Godeiro & Cipola, 2020	Seirinae	Cambodia	MT997754.1
14	<i>Seira tinguira</i> Cipola & Bellini, 2014	Seirinae	Brazil	MF716620.1
15	<i>Tyrannoseira bicolorcornuta</i> (Bellini, Pais & Zeppelini, 2009)	Seirinae	Brazil	MF716599.1
16	<i>Tyrannoseira raptora</i> (Zeppelini & Bellini, 2006)	Seirinae	Brazil	MF716610.1

Table 2. Partitioning scheme and substitution models selected by ModelFinder used for maximum likelihood analyses.

Partition	Genes	Model
1	ATP6 / NAD1 / ND4L	mtART
2	ATP8 / ND2 / ND6	mtART+F
3	COX1/ COX2 / COX3 / CYTB	mtART
4	ND3 / ND4 / ND5	mtART

et al. 2017). The partitions and models used are listed in Table 2. The Bayesian inference (BI) was performed using PhyloBayes-MPI v.1.8 (Lartillot et al. 2013), default model CAT+GTR with four rate categories, discretized gamma distribution of rates across sites, sampling every 100 generations, with the first 1000 sampled trees discarded as “burn-in”. Two Markov Chain Monte Carlo (MCMC) chains were run until the likelihood had satisfactorily converged (maxdiff < 0.3). Phylogenetic trees were visualized in Figtree v.1.3.1 (Rambaut 2016).

Results

Mitochondrial genomes of *Seira pallidipes* and *S. ferrarii* have 14,856 bp and 14,916 bp in length, respectively (Figs 2, 3). All 13 PCGs, 2 rRNAs, and 22tRNAs were found. In *S. ferrarii*, the direction of transcription was anti-clockwise, and a rare gene translocation was observed in the region ranging from 8337 bp to 8550 bp. The order of tTNAs is normally tRNA-Asn (trnN) → tRNA-Ser 1 (trnS1) → tRNA-Glu (trnE), but in *S. ferrarii*, the gene order is tRNA-Ser 1 (trnS1) → tRNA-Glu (trnE) → tRNA-Asn (trnN), meaning that a translocation happened in the position of trnN (Figs 1, 3). For this reason, *S. ferrarii* does not present the Pancrustacean ancestral gene order, like most mitogenomes of Seirinae se-

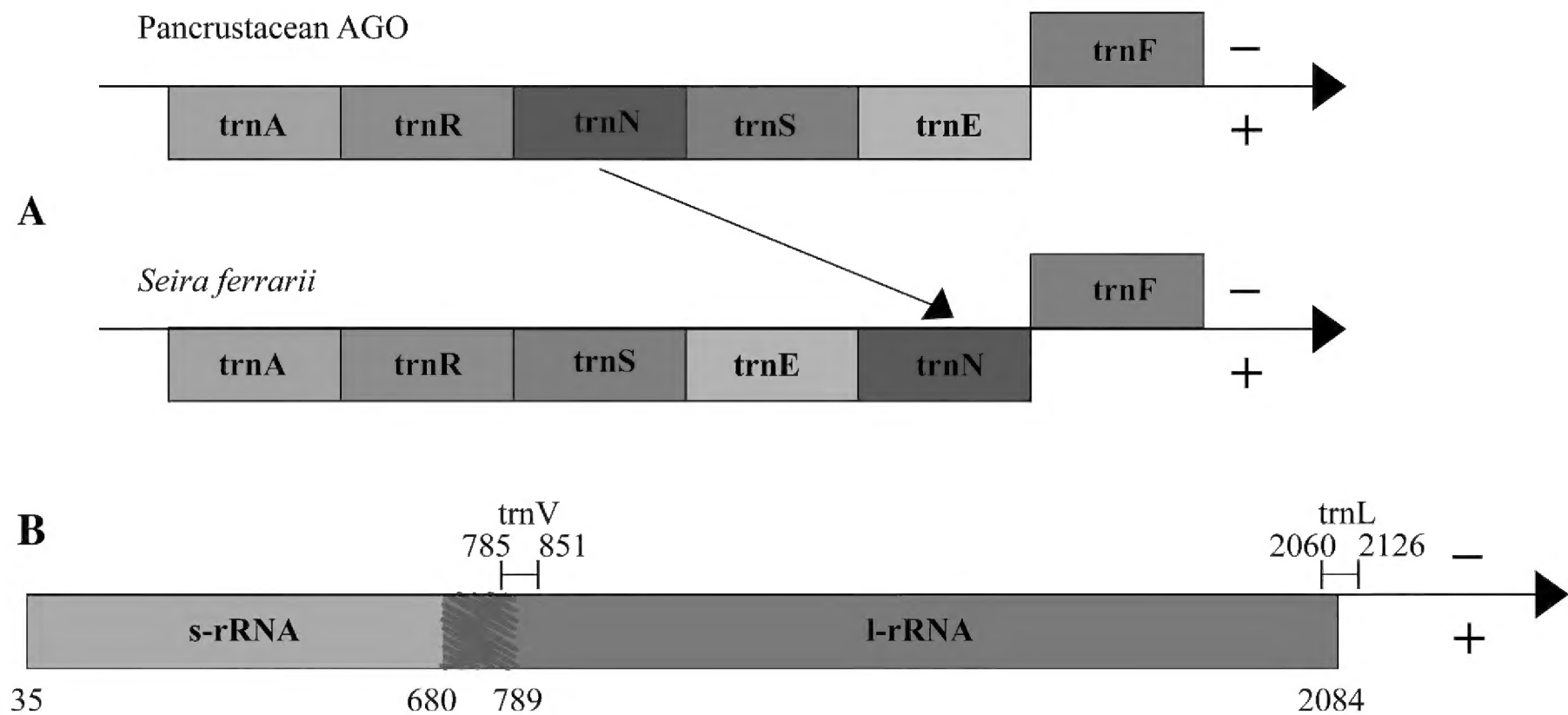


Figure 1. A gene order comparison between Pancrustacean and *Seira ferrarii* (clockwise direction) B region comprising rRNAs of *S. ferrarii* mitogenome (anti-clockwise direction). Scratch indicates the overlap between genes. Numbers represent the location of the genes in base pairs.

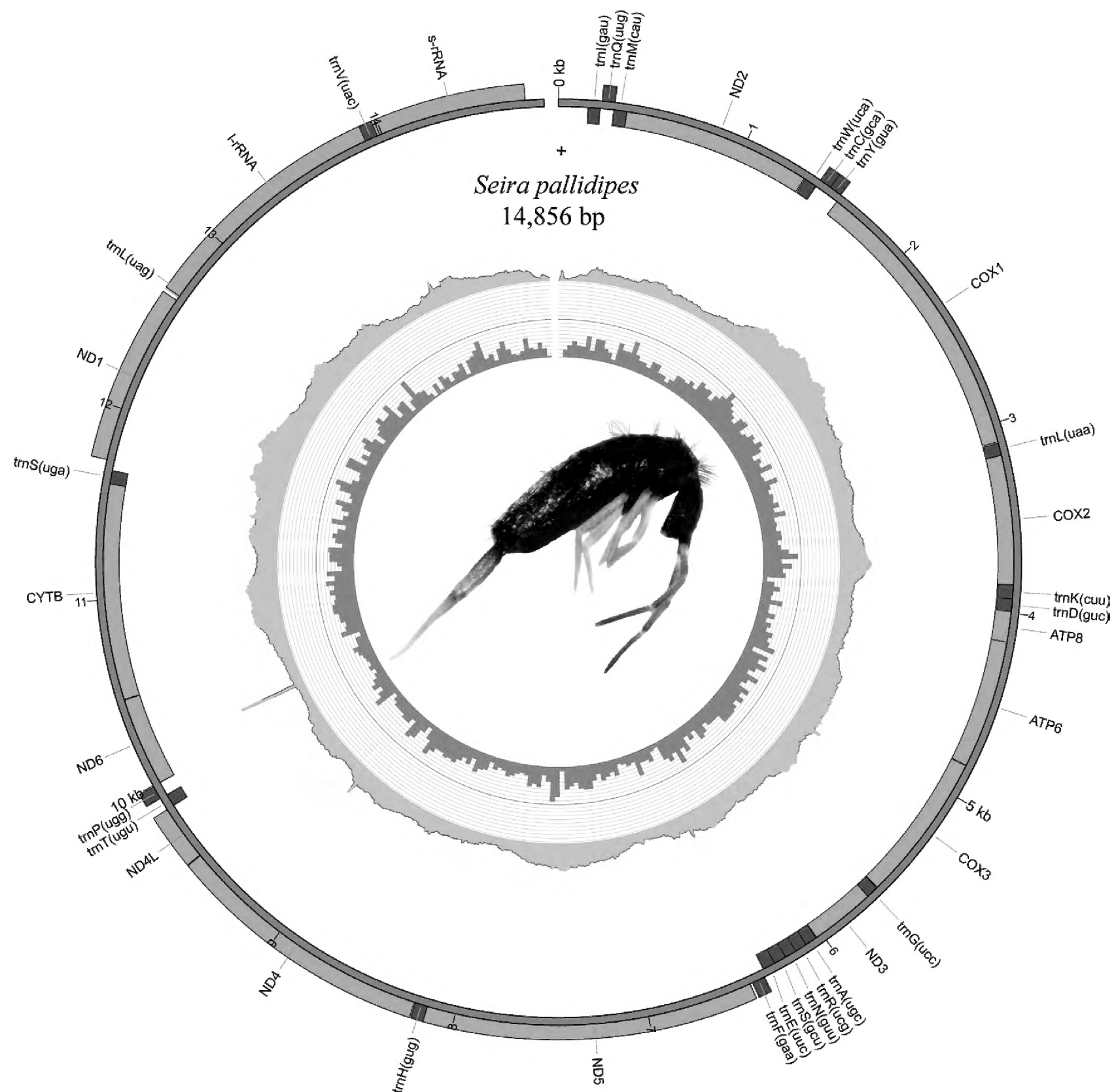


Figure 2. Circular representation of the mitogenome of *Seira pallidipes*. The innermost circle shows the GC content; the middle circle shows the reads coverage, and the outermost circle shows the gene features, rRNA, tRNA, and CDS. Photo in the center represents the original coloration of a specimen preserved in ethanol.

quenced until now, including *S. pallidipes*. Another interesting characteristic observed during the mitogenome analysis were long overlaps between the genes tRNA-Leu (*trnL*), 16S ribosomal RNA (*l-rRNA*), tRNA-Val (*trnV*), 12S ribosomal RNA (*s-rRNA*), with *trnV* totally inserted on the *l-rRNA* sequence (Figs 1–3). These overlaps were observed in all Seirinae mitogenomes sequenced to date but have never been reported before. A broader study needs to be carried out to compare the gene order of other Collembola taxa to verify whether these differences have significant evolutionary importance and phylogenetic signals.

The most common start-stop codons in *S. pallidipes* were ATT/ATG-TAA, and in *S. ferrarii* ATT/ATA-TAA (Tables 3, 4). This pattern is the most common in Collembola mitogenomes (Godeiro et al. 2022). AT-rich regions have lengths of 185bp and 421bp in *S. pallidipes* and *S. ferrarii*, respectively. The nucleotide composition of both mitogenomes presented higher AT content than other Seirinae mitogenomes, 78% in *S. pallidipes* and 80% in *S. ferrarii*.

Table 3. Gene order and features of the mitochondrial genome of *Seira pallidipes*.

<i>Seira pallidipes</i> – 14,856 bp					
Start	End	Length(bp)	Direction	Start/End code	Gene product [gene name]
155	219	65	+		tRNA-Ile [trnI(gau)]
225	293	69	-		tRNA-Gln [trnQ(uug)]
290	359	70	+		tRNA-Met [trnM(cau)]
359	1354	996	+	ATG/TAA	NADH dehydrogenase subunit 2 [ND2]
1361	1429	69	+		tRNA-Trp [trnW(uca)]
1429	1492	64	-		tRNA-Cys [trnC(gca)]
1492	1558	67	-		tRNA-Tyr [trnY(gua)]
1563	3098	1536	+	ATT/TAA	cytochrome c oxidase subunit I [COX1]
3105	3171	67	+		tRNA-Leu [trnL(uaa)]
3171	3851	681	+	ATA/TAA	cytochrome c oxidase subunit II [COX2]
3853	3925	73	+		tRNA-Lys [trnK(cuu)]
3925	3991	67	+		tRNA-Asp [trnD(guc)]
3991	4158	168	+	ATT/TAA	ATP synthase F0 subunit 8 [ATP8]
4152	4832	681	+	ATG/TAG	ATP synthase F0 subunit 6 [ATP6]
4835	5623	789	+	ATG/TAA	cytochrome c oxidase subunit III [COX3]
5627	5690	64	+		tRNA-Gly [trnG(ucc)]
5690	6034	345	+	ATT/TAA	NADH dehydrogenase subunit 3 [ND3]
6039	6100	62	+		tRNA-Ala [trnA(ugc)]
6100	6164	65	+		tRNA-Arg [trnR(ucg)]
6163	6228	66	+		tRNA-Asn [trnN(guu)]
6225	6292	68	+		tRNA-Ser 1 [trnS1(gcu)]
6292	6358	67	+		tRNA-Glu [trnE(uuc)]
6370	6439	70	-		tRNA-Phe [trnF(gaa)]
6452	8146	1695	-	ATA/TAA	NADH dehydrogenase subunit 5 [ND5]
8148	8213	66	-		tRNA-His [trnH(gug)]
8218	9567	1350	-	ATG/TAA	NADH dehydrogenase subunit 4 [ND4]
9571	9843	273	-	ATT/TAA	NADH dehydrogenase subunit 4L [ND4L]
9855	9925	71	+		tRNA-Thr [trnT(ugu)]
9925	9995	71	-		tRNA-Pro [trnP(ugg)]
9997	10467	471	+	ATT/TAA	NADH dehydrogenase subunit 6 [ND6]
10470	11609	1140	+	ATG/TAA	cytochrome b [CYTB]
11608	11674	67	+		tRNA-Ser 2[trnS2(uga)]
11675	12616	942	-	ATT/TAA	NADH dehydrogenase subunit 1 [ND1]
12617	12684	68	-		tRNA-Leu [trnL(uag)]
12651	14093	1443	-		16S ribosomal RNA [l-rRNA]
13908	13975	68	-		tRNA-Val [trnV(uac)]
13988	14758	771	-		12S ribosomal RNA [s-rRNA]
14778	107	185			AT-rich region

Our phylogenetic results placed the European population of the sampled *Seira* spp. as ancestral to the Asian and American populations mostly with high SH-aLRT support and Bayesian posterior probability (Fig. 4). The geographic proximity on this scale can lead to genetic adaptation for specific conditions (e.g., different climate, habitat) and can result in a striking level of genetic differentiation within a genus, as observed in the case of *Seira*.

Table 4. Gene order and features of the mitochondrial genome of *Seira ferrarii*.

<i>Seira ferrarii</i> – 14,916 bp					
Start	End	Length (bp)	Direction	Start/End code	Gene name
35	789	755	+		s-rRNA
785	851	67	+		trnV(uac)
680	2084	1405	+		l-rRNA
2060	2126	67	+		trnL(uag)
2126	3064	939	+	TTG/TAA	ND1
3055	3126	72	-		trnS2(uga)
3125	4261	1137	-	ATG/TAA	CYTB
4264	4758	495	-	ATA/TAA	ND6
4749	4815	67	+		trnP(ugg)
4815	4879	65	-		trnT(ugu)
4881	5159	279	+	ATT/TAA	ND4L
5159	6502	1344	+	ATA/TAA	ND4
6502	6568	67	+		trnH(gug)
6568	8259	1692	+	ATT/T--	ND5
8267	8333	67	+		trnF(gaa)
8337	8406	70	-		trnN(guu)
8409	8481	73	-		trnE(uuc)
8483	8550	68	-		trnS1(gcu)
8553	8618	66	-		trnR(ucg)
8618	8678	61	-		trnA(ugc)
8680	9024	345	-	ATT/TAA	ND3
9025	9086	62	-		trnG(ucc)
9092	9880	789	-	ATG/TAA	COX3
9880	10557	678	-	ATG/TAA	ATP6
10551	10712	162	-	ATA/TAA	ATP8
10713	10780	68	-		trnD(guc)
10780	10851	72	-		trnK(cuu)
10851	11534	684	-	ATA/TAA	COX2
11535	11600	66	-		trnL(uaa)
11595	13133	1539	-	ATT/TAA	COX1
13135	13199	65	+		trnY(gua)
13205	13268	64	+		trnC(gca)
13267	13333	67	-		trnW(uca)
13333	14298	966	-	ATA/TGA	ND2
14316	14384	69	-		trnM(cau)
14390	14458	69	+		trnQ(uug)
14464	14527	64	-		trnI(gau)
14530	35	421			AT-rich region

Discussion

Most of the European *Seira* species are from the Mediterranean (e.g., Gama 1964; Gruia et al. 2000; Cipola et al. 2018a). As several phylogeographic studies and reviews have pointed out, the Mediterranean region (in particular, but not exclusively, Iberia, Italia, and the Balkans) was also important refugia for thermophilic species during glacial periods (e.g., Provan and Bennett 2008;

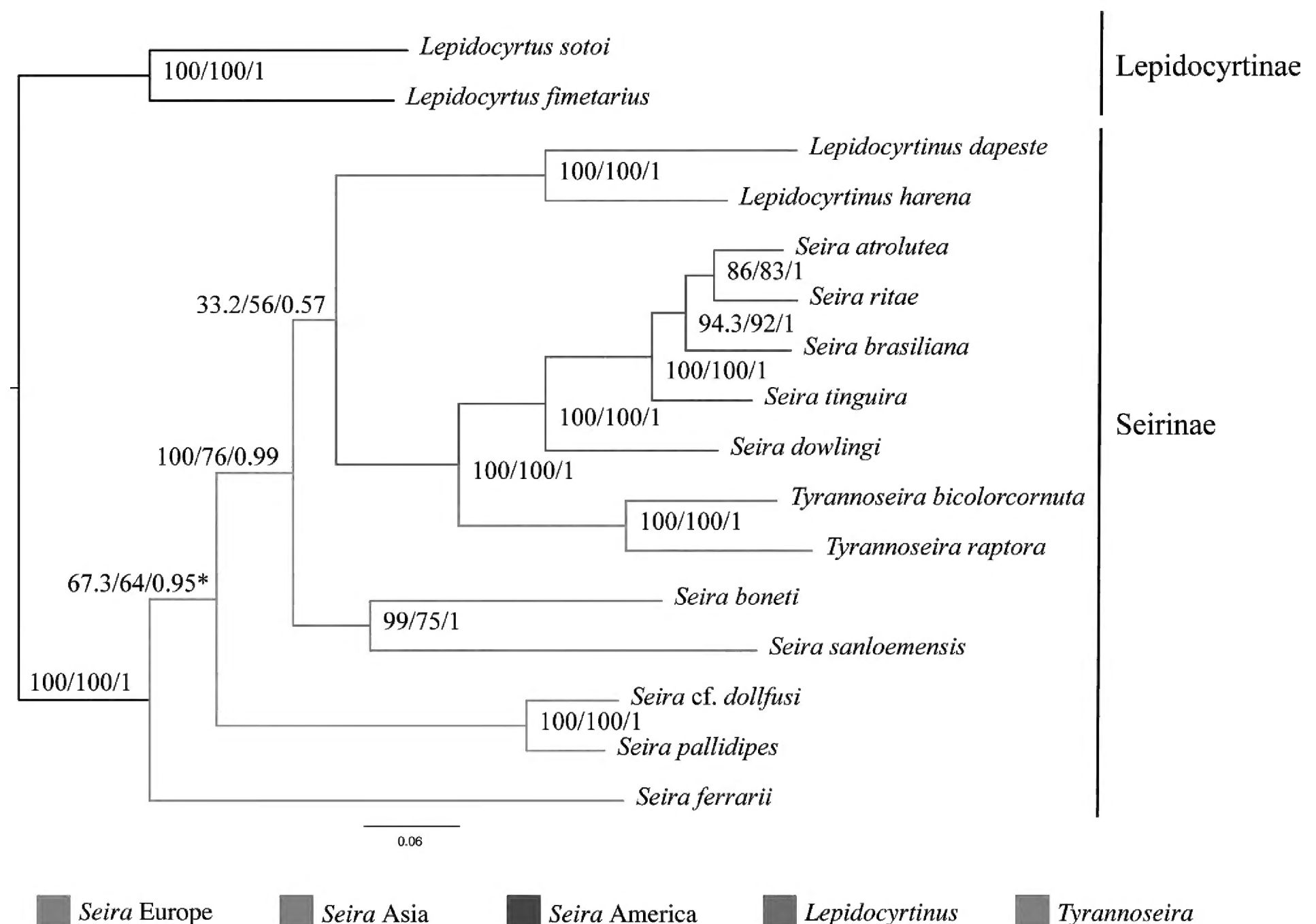


Figure 4. Phylogenetic placement of European *Seira*. Tree constructed based on maximum likelihood and Bayesian inferences (BI) from mitochondrial genomes. Numbers at the nodes represent the SH-aLRT support, bootstrap values (both for maximum likelihood), and the posterior probability (BI support), respectively. *In the BI the topology was: (*S. cf. dollfusi* + *S. pallidipes*) + *Seira ferrarii* + (other Seirinae).

position and the climatic conditions, the Carpathian Basin is rich in endemic and relict species (Varga 1995), and *S. pallidipes* may be one of its representatives.

Seira ferrarii represents a separate clade within Seirinae, while *S. pallidipes* with *S. cf. dollfusi* together form another clade (Fig. 4). The latter two species are more closely related morphologically by sharing a similar, mostly polichaetotic, dorsal macrochaetotaxy from Th II to Abd II, and are part of the “*squamornata*-group” sensu Cipola et al. (2018a). On the other hand, *S. ferrarii* shows a clear reduction in dorsal macrochaetotaxy and thus was classified in the so-called “*domestica*-group” sensu Jacquemart (1974). This kind of division of species groups established based on the macrochaetotaxy distribution can be observed in other derived genera of Entomobryomorpha, most notably in *Lepidocyrtus* (Mateos et al. 2018; Winkler et al. 2020).

This study is part of a larger initiative to better understand the dispersion pathways of Seirinae species. Systematic research on this subfamily is impacted by the scarcity of specialists based in other continents, with the exception of South America. Despite the limited taxon sample, our phylogeny (Fig. 4) pointed out that the genus *Seira* is not monophyletic, possibly should be subdivided into more genera, and that the morphology of the subfamily needs to be more deeply investigated.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

NNG designed the research, performed and analysed the data. DW collected the samples. NNG, YB and DW wrote the manuscript.

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Data availability

All accession numbers and links for the data that support the findings of this study are available in the main text.

References

- Barra JA (2004) Springtails of the genus *Seira* Lubbock, 1869 (Collembola: Entomobryidae) from Socotra Island. *Fauna of Arabia* 20: 399–408.
- Bedos A (2023) Fauna Europaea: *Seira*. In: Deharveng L (Ed.) Fauna Europaea: Collembola. Fauna Europaea version 2.6. <http://www.fauna-eu.org> [Accessed 6 June 2023]
- Bellini BC, Zhang F, de Souza PGC, dos Santos-Costa RC, Medeiros Gd S, Godeiro NN (2023) The evolution of Collembola higher taxa (Arthropoda, Hexapoda) based on mitogenome data. *Diversity* 15(1): 1–7. <https://doi.org/10.3390/d15010007>
- Carl J (1899) Notice descriptive des Collembolés de la collection de M. Adrien Dollfus recueillis a Lyons-la-Forêt (Eure) et dans d'autres localités de France et de Suisse. *Feuille jeune Naturalistes* 29(342): 95–100.
- Cicconardi F, Nardi F, Emerson BC, Frati F, Fanciulli PP (2010) Deep phylogeographic divisions and long-term persistence of forest invertebrates (Hexapoda: Collembola) in the North-Western Mediterranean basin. *Molecular Ecology* 19(2): 386–400. <https://doi.org/10.1111/j.1365-294X.2009.04457.x>
- Cipola NG, Morais JW, Bellini BC (2014) A new species of *Seira* (Collembola: Entomobryidae: Seirini) from Northern Brazil, with the addition of new chaetotaxic characters. *Zoologia* 31(5): 489–495. <https://doi.org/10.1590/S1984-46702014000500009>

- Cipola NG, Arbea J, Baquero E, Jordana R, de Moraes JW, Bellini BC (2018a) The survey of *Seira* Lubbock, 1870 (Collembola, Entomobryidae, Seirinae) from Iberian Peninsula and Canary Islands, including three new species. *Zootaxa* 4458(1): 1–66. <https://doi.org/10.11646/zootaxa.4458.1.1>
- Cipola NG, de Moraes JW, Bellini BC (2018b) Three new species of *Seira* Lubbock (Collembola, Entomobryidae, Seirinae) from Madagascar with *Lepidocyrtus*-like habitus. *Zootaxa* 4521(2): 151–173. <https://doi.org/10.11646/zootaxa.4084.2.1>
- Costa D, Timmermans MJTN, Sousa JP, Ribeiro R, Roelofs D, Van Straalen NM (2013) Genetic structure of soil invertebrate populations: Collembolans, earthworms and isopods. *Applied Soil Ecology* 68: 61–66. <https://doi.org/10.1016/j.apsoil.2013.03.003>
- Criscuolo A, Gribaldo S (2010) BMGE (Block Mapping and Gathering with Entropy): A new software for selection of phylogenetic informative regions from multiple sequence alignments. *BMC Evolutionary Biology* 10(1): e210. <https://doi.org/10.1186/1471-2148-10-210>
- Fiera C, Habel JC, Kunz M, Ulrich W (2017) Large-scale phylogenetic structure of European springtails (Collembola) depends on species range size and postglacial colonization history. *Biological Journal of the Linnean Society. Linnean Society of London* 120(3): 664–674. <https://doi.org/10.1111/bij.12907>
- Gama da MM (1964) Colêmbolos de Portugal Continental. *Memorias e estudos do Museu Zoologico da Universidade de Coimbra* 292: 1–252.
- Godeiro NN, Bellini BC (2014) Three new species of *Seira* Lubbock (Collembola, Entomobryidae) from Caatinga Domain, northeastern Brazil. *Zootaxa* 3764(2): 131–151. <https://doi.org/10.11646/zootaxa.3764.2.2>
- Godeiro NN, Pacheco G, Liu S, Cipola NG, Berbel-filho WM, Zhang F, Gilbert MTP, Bellini BC (2020) Phylogeny of Neotropical Seirinae (Collembola, Entomobryidae) based on mitochondrial genomes. *Zoologica Scripta* 49(3): 329–339. <https://doi.org/10.1111/zsc.12408>
- Godeiro NN, Bellini BC, Ding N, Xu C, Ding Y, Zhang F (2021) A mitogenomic phylogeny of the Entomobryoidea (Collembola): A comparative perspective. *Zoologica Scripta* 50(5): 658–666. <https://doi.org/10.1111/zsc.12487>
- Godeiro NN, Xu C, Zhang G, Zhang F (2022) Mitogenomic features of three species of Entomobryoidea (Collembola) from China. *Zootaxa* 5120(2): 283–288. <https://doi.org/10.11646/zootaxa.5120.2.8>
- Godeiro NN, Bu Y, Nilsai A, Deharveng L, Cipola NG (2023) Systematics of *Lepidocyrtinus boneti* Denis, 1948 (Collembola, Seirinae) reveals a new position for the species within Seirinae. *ZooKeys* 1152: 97–118. <https://doi.org/10.3897/zookeys.1152.99161>
- Gómez A, Lunt D (2007) Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula. In: Weiss F (Ed.) *Phylogeography of Southern European Refugia*. Springer, Netherlands, 155–188. https://doi.org/10.1007/1-4020-4904-8_5
- Gruia M, Poliakov D, Broza M (2000) Collembola of Northern Israel, II. (Special Papers in Honor of late Professor Ryozyo Yoshii). *Contributions from the Biological Laboratory. Kyoto University* 29(2): 117–131.
- Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology* 59(3): 307–321. <https://doi.org/10.1093/sysbio/syq010>
- Hewitt GM (2011) Mediterranean Peninsulas: the evolution of hotspots. In: Zachos FE, Habel JC (Eds) *Biodiversity Hotspots*. Springer, Berlin, 123–147. https://doi.org/10.1007/978-3-642-20992-5_7

- Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the Ultrafast Bootstrap Approximation. *Molecular Biology and Evolution* 35(2): 518–522. <https://doi.org/10.1093/molbev/msx281>
- Jacquemart S (1974) Resultats de la mission Anthropologique Belge au Niger. Collemboles nouveaux du Sahara. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 50(6): 1–46.
- Jacquemart S, Jacques JM (1980) A propos d'un Collembole Entomobryen a la fois marin et désertique. *Annales de la Société Royale Zoologique de Belgique* 109: 9–18.
- Jordana R, Arbea JI, Simón C, Lucíañez MJ (1997) Fauna Iberica (Vol. 8). Collembola, Poduromorpha (1st Edn.). Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, 807 pp.
- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14(6): 587–589. <https://doi.org/10.1038/nmeth.4285>
- Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20(4): 1160–1166. <https://doi.org/10.1093/bib/bbx108>
- Lartillot N, Rodrigue N, Stubbs D, Richer J (2013) PhyloBayes MPI: Phylogenetic reconstruction with infinite mixtures of profiles in a parallel environment. *Systematic Biology* 62(4): 611–615. <https://doi.org/10.1093/sysbio/syt022>
- Loksa I, Loksa I (1994) Adatok a Tétényi-fennsík ízeltlábú faunájához. In: Simon T (Ed.) Természeti Kincsek Dél-Budán. A Tétényi-Fennsík és a Háros-Sziget Növény- És Állatvilága, Természetvédelme. Cserépfalvi Kiadó – Zöld Jövő Környezetvédelmi Egyesület, Budapest, 40–51.
- Lubbock J (1870) Notes on the Thysanura. – Part IV. The Transactions of the Linnean Society of London (Vol. XXXII, Part the Second, M.DCCC.LXX), Read June 3rd, 1869, 277–297. <https://doi.org/10.1111/j.1096-3642.1870.tb00214.x>
- Mari Mutt JA (1986) Puerto Rican species of *Seira* (Collembola: Entomobryidae). *Caribbean Journal of Science* 22(3–4): 145–158.
- Mateos E, Escuer P, Busmachiu G, Riutort M, Álvarez-Presas M (2018) Untangling *Lepidocyrtus* (Collembola, Entomobryidae): New molecular data shed light on the relationships of the European groups. *Invertebrate Systematics* 32(3): 639–651. <https://doi.org/10.1071/IS17056>
- Meng G, Li Y, Yang C, Liu S (2019) MitoZ: A toolkit for animal mitochondrial genome assembly, annotation and visualization. *Nucleic Acids Research* 47(11): e63. <https://doi.org/10.1093/nar/gkz173>
- Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R (2020) IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. *Molecular Biology and Evolution* 37(5): 1530–1534. <https://doi.org/10.1093/molbev/msaa015>
- Parona C (1888) Res Ligusticae VI. Collembole e Tisanuri finora riscontrante in Liguria. *Annali del Museo civico di storia naturale di Genova, Serie 2a*(6): 133–154.
- Provan J, Bennett K (2008) Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology & Evolution* 23(10): 564–571. <https://doi.org/10.1016/j.tree.2008.06.010>
- Rambaut A (2016) FigTree v. 1.4.3. <http://tree.bio.ed.ac.uk/software/figtree/> [Accessed 1 June 2023]
- Reuter OM (1895) Species nova generis Poduridarum *Sira* Lubb. *Wiener Entomologische Zeitung* 14: e114.

- Smirnov V, Warnow T (2021) MAGUS: Multiple sequence alignment using graph clustering. *Bioinformatics* 37(12): 1666–1672. <https://doi.org/10.1093/bioinformatics/btaa992>
- Stach J (1929) Verzeichnis der Apterygogenea Ungarns. *Annales Historico-Naturales Musei Nationalis Hungarici* 26: 269–312.
- Steenwyk JL, Buida TJ III, Labella AL, Li Y, Shen X-X, Rokas A (2021) PhyKIT: A broadly applicable UNIX shell toolkit for processing and analyzing phylogenomic data. *Bioinformatics* 36(16): 2325–2331. <https://doi.org/10.1093/bioinformatics/btab096>
- Tosi L, Parisi V (1990) *Seira tongiorgii*, a new species of Collembola from a volcanic environment. *Bolletino di zoologia* 57(3): 277–281. <https://doi.org/10.1080/11250009009355708>
- Varga Z (1995) Geographical patterns of biological diversity in the Palearctic region and the Carpathian Basin. *Acta Zoologica Academiae Scientiarum Hungaricae* 41(2): 71–92.
- Wang HC, Susko E, Roger AJ (2019) The relative importance of modeling site pattern heterogeneity versus partition-wise heterotachy in phylogenomic inference. *Systematic Biology* 68(6): 1003–1019. <https://doi.org/10.1093/sysbio/syz021>
- Winkler D, Dányi L (2017) Redescription of *Seira pallidipes* Reuter, 1895 and its synonymization with *Seira pillichii* Stach, 1930 (Collembola, Entomobryidae, Seirini). *Zootaxa* 4312(3): 497–514. <https://doi.org/10.11646/zootaxa.4312.3.5>
- Winkler D, Mateos E, Traser G, Lakatos F, Tóth V (2020) New Insight into the Systematics of European *Lepidocyrtus* (Collembola: Entomobryidae) Using Molecular and Morphological Data. *Insects* 11(5): e302. <https://doi.org/10.3390/insects11050302>
- Yosii R (1959) Collembolan fauna of the Cape Province, with special reference to the genus *Seira*. *Biological Results of the Japanese Antarct Research Expedition* 6(6): 1–24. <https://doi.org/10.5134/176436>
- Yu D, Ding Y, Tihelka E, Cai C, Hu F, Liu M, Zhang F (2022) Phylogenomics of elongate-bodied springtails reveals independent transitions from aboveground to belowground habitats in deep-time. *Systematic Biology* 71(5): 1023–1031. <https://doi.org/10.1093/sysbio/syac024>